THE FOOD PUMP OF *PELOCORIS* AND COMPARATIVE STUDIES ON OTHER AQUATIC HEMIPTERA

By Edwin P. Marks

Washburn University, Topeka, Kansas

Introduction

In earlier studies it has been found that in the Corixidae (Griffith 1945, Sutton 1951, Benwitz 1956, Marks 1958) and in the Notonectidae (Marks 1958) the buccopharyngeal pumps contain rather complicated armatures apparently derived from the remnants of the hypopharyngeal suspensorium. When the opportunity was provided to study this closely related form, therefore, it was quickly accepted. Twelve specimens of *Pelocoris femoratus* P.B. from ponds in the Cambridge, Mass. area were obtained. Several were killed in chloroform and dissected immediately. Three were cleared in caustic, lightly stained in acid fuchsin, and placed in glycerin. The last makes an excellent medium for dissection of both cleared and uncleared specimens because of both its property of rendering the material transparent, and its viscosity, which holds the specimen in place for drawing or photographing. The dissections were photographed by Dr. Thomas S. Parsons and then drawn by the author for the purpose of illustration.

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Description

When the ventral wall of the head is removed, the muscles of the stylets are exposed. These muscles and the attached stylets can be removed by gently withdrawing them from their attachments and sliding them out of the

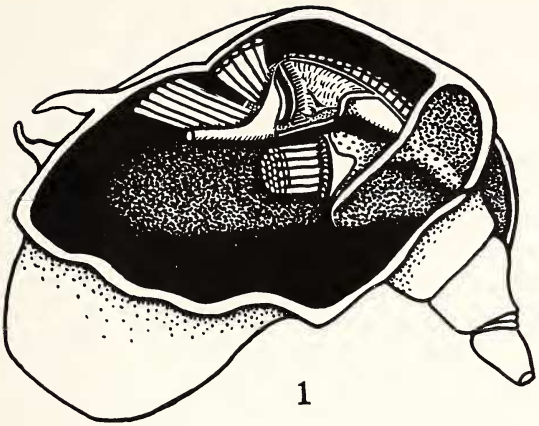
beak. This exposes the salivary pump, which is firmly embraced by the ventral arms of the hypopharynx (Plate 11, Fig. 1). The latter hold it in place and enclose the short duct leading to the stylets. The pump itself closely resembles that of *Belostoma* (Marks 1958). It is rather large and heavily constructed, which is somewhat surprising in so small a bug. The pump is operated by two powerful muscles which insert on the forked apodeme of the plunger of the pump and originate on the wings of the hypopharynx, one on either side of the food pump.

The food pump itself is found dorsal to the salivary pump, partially obscured by the latter and by the arms of the hypopharynx. Both of these can be removed by gently pulling them away. This exposes the ventral wall of the food pump for its entire length. From the ventral aspect it is somewhat triangular in shape (Plate 11, Fig. 1). It begins at the anterior end as a sheath around the food channel and widens gradually into the anterior or cibarial portion of the pump. This region extends approximately one half of the length of the pump. At this point it flares laterally to form the heavily scerotized pharyngeal portion of the pump. There is a dark, heavily sclerotized bar in this region which is visible through the floor of the pump. It arises from the dorso-lateral edges, and arches ventrally crossing the pump just in front of its widest point. This

Explanation of Plate 10.

The head of *Pelocoris femoratus* P.B. Figure 1. Composite stereogram showing structure of pump and relationship with the rest of the head. Figure 2. Parasagittal section showing the lateral aspects of the food and salivary pumps. Figure 3. Sagittal section slightly lateral to the midline, showing the internal structure of the food and salivary pumps.

Abbreviations Used in Plates: AB — anterior sclerotized bar; AH — arms of hypopharynx; AP — apodeme of salivary pump; BP — bristle pouch; CM — cibarium; ES — esophagus; FG — frontal ganglion; FP — food pump; FR — floor of pump; G.1 — muscle group 1; G.2 — muscle group 2; G.3 — muscle group 3; HX — hypopharynx; LF — lateral fold; PB — posterior sclerotized bar; PX — pharynx; SB — sclerotized bar; SP — salivary pump; ST — setae-like teeth; TF — transverse fold; T.1 — first toothed fold; T.2 — second toothed fold; WH — wing of the hypopharynx.



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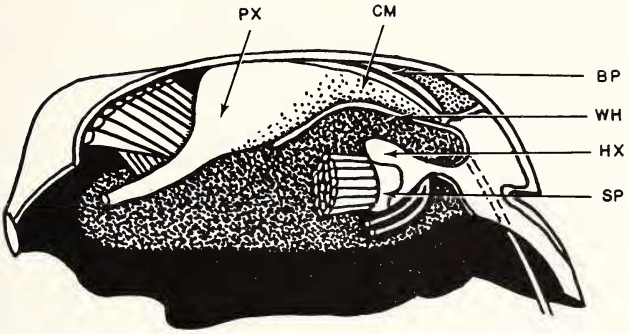

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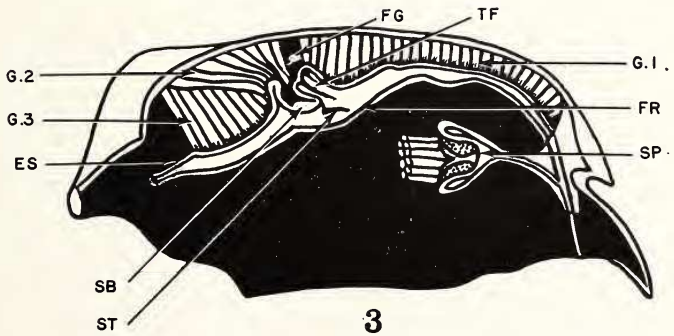

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MARKS — PELOCORIS FEMORATUS P. B.

bar, however, belongs properly to the roof of the pump and will be described in detail later on. From this point the walls of the pump taper sharply, converging to form the entrance of the esophagus.

From a lateral view (Plate 10, Fig. 2) the pump is obscured at its juncture with the cranium, by the presence of the bristle pouches, which must be cut away to permit adequate inspection of the structures. The cibarial portion of the pump expands gradually for approximately half of the entire length. Then it bends ventrally, forming the enlarged pharyngeal portion in which the sclerotized bar is again plainly visible through the wall. Directly behind the bar, the dorsal edge of the ventral wall detaches from the cranium and descends to form the entrance to the esophagus. The large pharyngeal dilator muscles emerge below the esophagus at this point and attach to the posterior wall of the cranium.

If a head is placed on a block of paraffin with the dorsal side up and sectioned free hand along the midsagittal line with a very sharp blade, the two halves can be separated and examined under a stereoscopic microscope. If one half is placed in glycerin for a few hours, the tissues will partially clear showing the sclerotized structures in sharp relief. The other half preserved in alcohol will be better for the study of the muscles themselvs. Specimens fixed for a few hours in alcoholic Bouin's solution were used in studying the frontal ganglion as the picric acid in this fixative stains the muscles darker than it does the nervous tissue. The structures as seen in such a dissection are shown in Plate 10, fig. 3.

There are three discrete groups of muscles which operate the food pump. The first group, which is distinctly cibarial in origin, operates the delicate anterior portion of the pump. These muscles arise on the striated inner surface of the cranium and insert by means of slender sclerotized apodemes on the midline of the roof of the pump. The action of these muscles is obvious and direct. They raise the roof of the food channel and thus draw food from the stylets into the pump. This group of muscles, which will be referred to as "Group 1", consists of the dilators

of the cibarium, and they extend approximately one half of the length of the pump. The second group of muscles is both longer and heavier than the first. It arises on the posterior angle of the cranium and inserts on a large apodeme, which attaches in turn to the sclerotized bar in the dorsal wall of the pump. This group of muscles lies behind the frontal ganglion and thus must represent the anterior dilators of the pharynx. These muscles will be referred to as "Group 2". They occupy approximately one-fourth of the length of the pump. The action of these muscles appears from micromanipulation to result in a rocking motion of the sclerotized bar so that the attached teeth sweep the floor of the pump. The third group of muscles is somewhat smaller than the others. These muscles, like the first group, insert on the midline of the roof of the pump by means of slender sclerotized apodemes. The muscles are somewhat longer and more slender than Group 1. They originate on the posterior angle of the vertex and make up the final one-fourth of the length of the pump. They serve to dilate the posterior pulsatile area, which carries food into the esophagus, and represent the posterior pharyngeal dilators. They will be referred to as "Group 3".

The membrane which makes up the roof of the pump varies in structure in the three portions of the pump. In the anterior portion, which is operated by the muscles of Group 1, the roof is a delicate membrane which is V-shaped in cross section. The dorsolateral edges are attached at the lateral margins of the pump and the dilator muscles are attached at the midline. This membrane is otherwise uncomplicated for the first one-third of its length. At this point an oblique fold appears in the lateral walls (Plate 11, Fig. 4) and extends dorsally and posteriorly nearly to the lateral edges. The walls of this fold are more heavily sclerotized than the surrounding area and are yellow-brown in color. The folds form a distinct landmark in the membrane. They possess no musculature, and will be called the lateral folds of the cibarium.

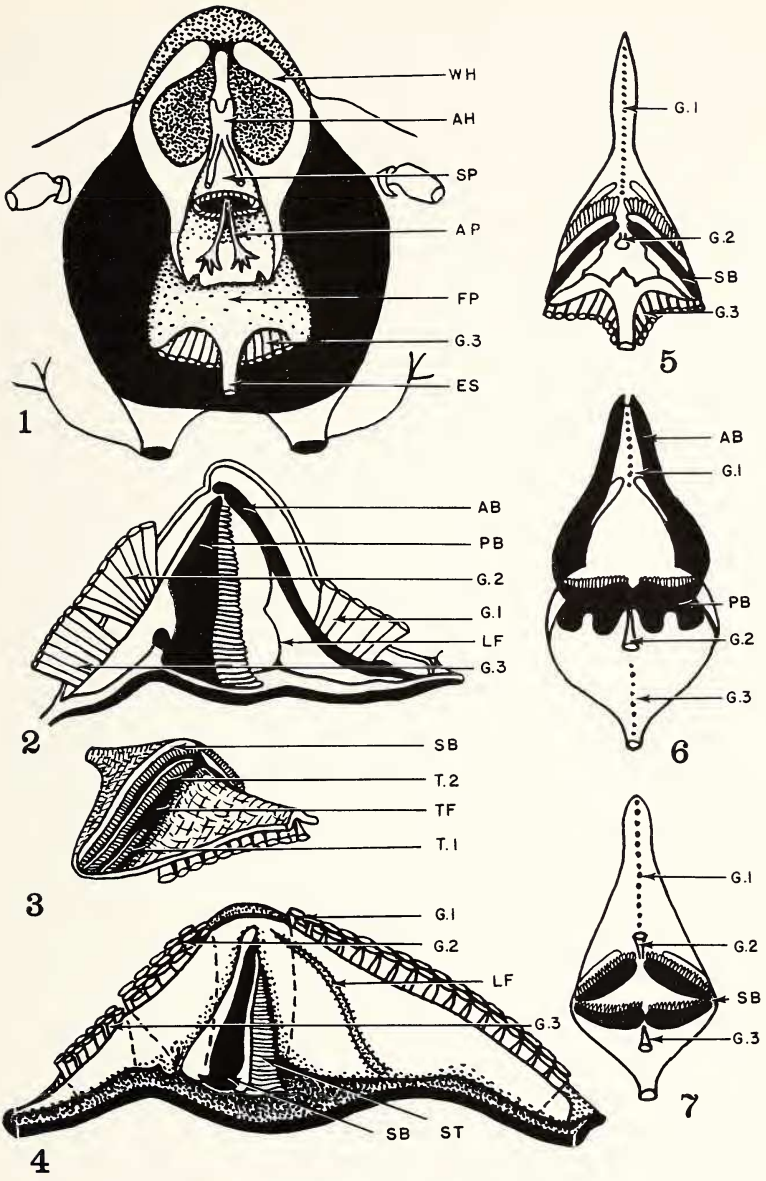
Posterior to these folds, the membrane curves dorsally, forming a deep transverse fold (Plate 11, Fig. 4). This fold contains in its cavity a series of secondary folds which

are provided with toothed armatures (Plate 11, Fig. 3). The setae-like teeth are borne on lightly sclerotized ridges, which cross the membrane. There are three such ridges, the first of which is incomplete, extending only part way down the sides of the pump. The second ridge extends downward to the midline. These two ridges are completely enclosed in the transverse fold, and show only in a sagittal section, or when this fold is pulled open for inspection. The third ridge is the heaviest of all and occurs on the posteroventral edge of the fold where it is visible in the ventral or lateral view. This ridge is closely attached by a membrane to the heavily sclerotized transverse bar which lies immediately behind it. This bar is perhaps the most prominent structure in the dorsal wall. It consists of a heavily pigmented and sclerotized thickening in the dorsal membrane. It is comma-shaped in sagittal section with the tail of the comma extending dorsally and anteriorly. The toothed fold is attached by a membrane to this forward edge. At the posterior edge of the bar is found a second, less heavily sclerotized bar which is, in turn, attached to the one in front by a thin membrane. This second bar is provided with a large hollow apodeme on which muscle Group 2 inserts. Posterior to this apodeme, the roof of the pump becomes membranous again, closely resembling the structure found in the cibarial portion. It is V-shaped in cross section and the muscles attach along the midline by means of slender sclerotized apodemes. This region narrows sharply to form the entrance to the esophagus.

The floor of the pump is relatively simple. It is heavily and uniformly sclerotized along its entire length. As can

Explanation of Plate 11.

Figure 1. Ventral view of the food and salivary pumps of *Pelocoris*. Figure 2. Lateral view of the food pump of *Notonecta* with the lateral wall of the floor of the pump cut away. Figure 3. Ventral aspect of the roof of the food pump of *Pelocoris* showing the transverse fold and the teeth. Figure 4. Lateral view of the food pump of *Pelocoris* with the lateral wall of the pump cut away. Figure 5. Ventral view of the roof of the pump of *Pelocoris* showing the armature and the lateral fold. Figure 6. Dorsal aspect of the roof of the pump of *Notonecta*. Figure 7. Dorsal aspect of the roof of the pump of *Hesperocorixa*.



MARKS — HEMIPTERAN FOOD PUMP

be seen in Plate 10, Fig. 2, it forms the rigid framework which permits an effective pumping action. With patience and care the floor of the pump can be loosened at the edges and gently lifted off. This exposes the ventral aspect of the roof of the pump, not otherwise visible. The structures exposed are shown in Plate 11, Fig. 5. Here one can see the relationships of the hard parts to the membrane and open up the transverse fold to expose the first and second toothed ridges, as shown in Plate 11, Fig. 3. Plate 11, Fig. 4, shows a lateral view with the side of the floor of the pump cut away. Here the setae-like teeth are seen in detail. They are strikingly like those found in *Notonecta,* which are shown in Plate 11, Fig. 2. Note that, in *Pelocoris,* the teeth associated with this bar are not directly connected to it as in *Notonecta,* but are instead attached to it by means of a membrane. The sclerotized bar does not articulate with the floor at the lateral margins, but instead ends in a membranous connection. There is no dorsal bar in the cibarial region as there is in *Notonecta.*

The purpose of this pharyngeal armature is not fully understood. It is not clear from the action of the parts exactly what role they play in the ingestion of the food. It may be supposed that the teeth serve some sort of straining function and perhaps act to break up clots in the food material. When the apodeme is worked back and forth the second set of teeth appears to rub over the third set much as one might clean a comb with a brush. Such action might be supposed to prevent the clogging of the teeth with food material during feeding. The action of the first set of teeth, which extends only part way down the sides, has not been determined. Plate 10, Fig. 1, shows a composite stereogram of the entire structure with the lateral wall of the pump cut away. It will help the reader to orient the various structures in relationship one with another and with the head as a whole.

Discussion

A detailed comparison of the pumps of *Notonecta, Pelocoris,* and *Hesperocorixa* is necessary before any assumptions can be made concerning the relationships between

them. The reader is referred to the beautifully illustrated work of Benwitz (1956), and to the papers of Griffith (1945), Rawat (1939), Sutton (1951) and Marks (1958) for further information on these three groups. Since the subject of this paper is *Pelocoris,* it will serve as a point of reference and the other forms will be compared with it.

The cibarial portion of the food pump of *Pelocoris* is elongated as it is in the Corixidae, both groups having an elongated clypeal region. Correspondingly, in both groups the musculature of the cibarial region is highly developed and this region has assumed the largest part of the pumping function. In *Notonecta,* however, the clypeal region is relatively much shorter, and these muscles are only weakly developed. The pumping action is shared approximately evenly with the posterior pharyngeal pump. In all three insects there is a lateral oblique fold (Plate 11, Figs. 5, 6, and 7). This fold is figured by Rawat (1939) in *Naucoris* but is not mentionened in the text. It is not provided with muscles and appears to be a stiffening device enabling the entire membrane to respond to the pull of the muscles as a unit. Unfortunately Rawat's otherwise fine paper does not cover the pump of *Naucoris* in any detail.

The sclerotized armature is found posterior to this fold. In *Notonecta* the sclerotized, toothed bar is activated by a set of muscles which are apparently located anterior to the frontal ganglion (Griffith 1945). The position of this ganglion has been confirmed in this study. These muscles presumably represent the posterior cibarial dilators. In *Pelocoris* there is a strikingly similar toothed bar. The muscles which operate this latter bar, however, are behind the frontal ganglion and thus presumably represent the anterior pharyngeal dilators, raising some doubt that these two bars are actually homologous. In *Hesperocorixa* where there are two sets of bars (Plate 11, Fig. 7), the anterior bars are activated by the posterior cibarial dilators while the posterior set is activated by the anterior pharyngeal dilators, the frontal ganglion being located between the two apodemes. Sutton (1951) reports finding two types of food pumps in *Naucoris.* She describes the first type as follows: "Buccopharyngeal teeth are present, so similar in

appearance to those of the Corixidae that from the sections through the buccopharyngeal regions it would be almost impossible to tell which genus was being examined" (page 489). The second type she characterized by "the presence of a small number of uniform teeth in the buccopharyngeal region". From the figures (fig. 5, page 474, and fig. 6, page 475) it is obvious that *Pelocoris* most closely resembles the second type. In all twelve specimens examined, the pumping apparatus was identical, there being apparently only one variety of this species in this area. In no case were specimens found which might be confused with corixids.

In the three insects examined there is a second pulsatile area which lies posterior to the armature. This area reaches its greatest development in *Notonecta* where it is as well developed as the cibarial pump. In *Pelocoris* it attains a modest development, but is not nearly as prominent as in *Notonecta*. In *Hesperocorixa,* muscle Group 3 is reduced to a few strands at the entrance to the esophagus. In all cases these muscles are well behind the frontal ganglion and thus represent the posterior pharyngeal dilators. The action of this area is apparently to pass food on from the pharyngeal region into the esophagus.

It is difficult to establish homologies between the parts of the sclerotized armatures of the three insects. At first appearance, when the preparations are studied from a ventral view (Plate 11, Figs, 5, 6, and 7), the homologies would appear to be as follows:

a. The anterior lateral bars of *Notonecta* are unique and do not appear in the other groups.

b. The posterior transverse bar of *Notonecta* appears homologous with the anterior transverse bar of *Hesperocorixa*. Both are activated by the posterior cibarial dilators. Both possess similar teeth. Both are posterior to the lateral constriction and the lateral fold.

c. The sclerotized bar of *Pelocoris* appears to be homologous to the posterior transverse bar of *Hesperocorixa*. Both are activated by the anterior pharyngeal dilators. Both occur at the point of greatest width of the pump. In both cases the apodeme is attached to an area behind the bar rather than to the bar itself.

If, however, one compares the lateral views of the armatures (Plate 11, Figs. 2 and 4) of *Notonecta* and *Pelocoris*, one is forcefully struck by the similarity of the transverse bars in these two groups. So striking is this similarity that the author carefully rechecked the positions of the muscles in relationshp to the frontal ganglion. The question then arises as to whether, in spite of the diffierence in the origin of the muscles attached to these bars, they are not actually homologous. It is possible that the present musculature of this bar in *Notonecta* may be a secondary condition due to a posterior shifting of a group of the cibarial dilators. This would account for the position of the frontal ganglion as well as the reduction of the pharyngeal dilators to their present condition. If this were the case, then the transverse bar of *Notonecta* would be homologous with the posterior transverse bar of *Hesperocorixa* and the transverse bar of *Pelocoris*. All three of the bars would be pharyngeal in origin. The anterior transverse bar of *Hesperocorixa* would then be homologous with the second tooth-bearing fold found in the transverse fold of *Pelocoris*, both being definitely cibarial in origin. At the present time there is not sufficient evidence available to uphold or eliminate either of these hypotheses.

Certain of these relationships do, however, appear to be significant. Certainly the appearance of such similar structures in closely related groups can scarcely be coincidental. These structures then should be of some significance in ascertaining the relationships between groups. From the very slender evidence available at this time, it would appear that *Pelocoris* shows features pertaining to both the notonectids and corixids. It is like *Notonecta* in such features as the single, heavy, toothed bar, and the well developed pharyngeal pulsatile area, while it is more like *Hesperocorixa* in the presence of secondary toothed folds and the highly developed cibarial pulsatile region.

This evidence, inconclusive as it is, tends to bear out the suggestion of China (1955) that the Naucoridae occupy a place in the phylogeny of the Hemiptera which gives them fairly recent common ancestry with the Notonectidae

and the Corixidae, these two latter groups then pursuing diverging lines of specialization. Investigation of the pumps of various genera within these three families should provide valuable information concerning these relationships.

Literature Cited

Benwitz, G.

1956. Der Kopf von *Corixa punctata* Ill. (*geoffroyi* Leach) (Hemiptera - Heteroptera). Zool. Jahrb., Abt. Anat., 75:311-378.

China, W.E.

1955. The evolution of the water bugs. Bull. Nat. Inst. Sci. India, 7:91-103.

Griffith, M.E.

1945. The environment, life history, and structure of the water boatman *Rhamphocorixa acuminata* (Uhler) (Hemiptera, Corixidae). Univ. Kans. Sci. Bull., 30:241-365.

Marks, E.P.

1958. A comparative study of the foregut of several aquatic Hemiptera. J. Kans. Ent. Soc., 31:138-153.

Rawat, B.L.

1939. Notes on the anatomy of *Naucoris cimicoides* L. (Hemiptera-Heteroptera. Zool. Jahrb., Abt. Anat. 65:535-600.

Sutton, M.F.

1951. On the food, feeding mechanism and alimentary canal of Corixidae (Hemiptera, Heteroptera). Proc. Zool. Soc. Lond. 121:465-499.